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PROCEEDINGS OF THE
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OBSERVATIONS ON SOME PLESIONBIOTIC COLONIES OF ANTS
(HYMENOPTERA), WITH NOTES ON SOME OTHER MIXTO-
BIOTIC COLONIES

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IN June 1943, while staying at Porlock, Devon, the following species of ants were collected:—1. *Myrmica lobicornis* Nyl. 2. *Myrmica scabrinodis* Nyl. 3. *Myrmica laevinodis* Nyl. 4. *Myrmica ruginodis* Nyl. 5. *Acanthomyops (Donisthorpea) niger* L. 6. *Acanthomyops (Chthonolasius) flavus* F. 7. *Formica rufa* L. 8. *Formica fusca* L. and its var. *rubescens* F. Six of these species, together with *Formica fusca rubescens*, were found on the foreshore. No fewer than five different combinations of two species living together under the same stone were found to occur, as follows:—

1. { *Formica fusca rubescens* F.
 Acanthomyops (Chthonolasius) flavus F.
2. { *Acanthomyops (Donisthorpea) niger* L.
 Acanthomyops (Chthonolasius) flavus F.
3. { *Myrmica scabrinodis* Nyl.
 Acanthomyops (Chthonolasius) flavus F.
4. { *Formica fusca* L.
 Acanthomyops (Donisthorpea) niger L.
5. { *Formica fusca* L.
 Myrmica laevinodis Nyl.

Several examples of each of these combinations were found.

A number of different ways in which ant species live side by side, or mixed together, have been described. These have been classified and given names on several occasions, notably by Wheeler in 1910, whose classification is both a summary of the earlier systems and the one that is in most general use amongst myrmecologists today. He divides all such ant colonies into either (1) compound nests, or (2) mixed nests.

In the compound nests the brood is kept separate; in the mixed nests, it is not.

The compound nests are sub-divided as follows:—

(a) *Plesiobiosis*. The colonies are established close together, usually under the same stone, but entirely separately, often fighting when the stone is removed (see below).

(b) *Parabiosis*. The broods are separate, but the ants use the same "roads" when going out to forage. Forel (1898) first used this term to describe the

relationship of the Colombian *Crematogaster parabiotica* F. and *Dolichoderus debilis parabiotica* F. Wheeler also places here the colonies of ants nesting in different branches of the same tree.

(c) *Cleptobiosis*. Forel (1901) suggested that this term be restricted to those cases in which (to quote Wheeler *loc. cit.*) "small ants establish their nests near or on the nests of a larger species and either feed on the refuse or waylay the workers when they return home." This group includes many of the *DOLICHODERINAE*.

(d) *Lestobiosis*. Minute species of ants make their galleries in the walls of the nests of other larger species, living entirely separately, but stealing from the other ants, which cannot chase them into their small holes.

(e) *Phylacobiosis*. The ants live in termite nests and appear to be on friendly terms with their hosts, helping to defend the colony.

(f) *Xenobiosis*. Wheeler (1910) gave this name to the types of nest community in which "guests ants" occur; the relationship is of a compound nature, but very intimate, the "guests" never being found except in association with the host species. An example of xenobiosis is the occurrence of *Formicoxenus nitidulus* Nyl. in the nests of *Formica rufa* L.

Wheeler makes no similar classification of the mixed colonies, but follows the obvious divisions in describing the individual cases of temporary parasitism, slave-making, and permanent parasitism. In the case of temporary parasitism, the queen of the parasitic species enters the nest and either kills the host queen, or else this is done by the workers of the host species. The host species, therefore, dies out. The mixed colonies of the slave-workers are brought about by the capture of pupae of the slave species, which hatch out in the slave-makers' nest to form a mixed colony. The strength of the slave-species is kept up by constant raiding. In permanent parasitism, the queen of the host species may or may not be killed. In extreme cases, the workers are lacking in the host species (*Wheeleriella*, *Epoecus*, *Anergates*).

Although all these terms have been in use amongst myrmecologists for nearly thirty-five years, there is no specific term which includes all the various forms of commensalism amongst ants. Such terms as symbiosis and commensalism refer to a wider range of phenomena than those described above, while Wheeler has limited the use of the terms "Compound" and "Mixed" colonies.

It is therefore proposed that all types of mixed and compound nests of ants (and ants and termites) should be included in the new collective term *mixtobiosis*.

The Porlock plesiobiotic colonies.

All the five mixtobiotic colonies listed above are examples of plesiobiosis. Large flat stones were common on the foreshore and little shelter was available. There seems little doubt that most of these colonies were formed by females of the different species seeking the shelter of the same stone after the nuptial flight. Donisthorpe (1927), however, states that the "stealing habits of the *Myrmica scabrinodis* account for the fact that it is frequently met with near the nests of *Acanthomyops flavus* and in the nests of other ants." Certainly there are many records of such colonies of *scabrinodis* and *flavus* under the same stone, and perhaps the relationship in this case may be more nearly that of cleptobiosis. It is probable that the association was accidental in the first place. This transition from plesiobiosis to cleptobiosis is not, however, the normal occurrence in the case of the Dolichoderine scavengers, in which there is no true transition stage as in the case of the *Myrmica scabrinodis*. Similar

mixtobiotic colonies of *Myrmica* and *flavus* have been found near Bath—another district where there are large flat stones and little other shelter. In nearly all the Porlock colonies fighting occurred when the stone was lifted, being observed in all five combinations.

Observations on some other mixtobiotic colonies of ants.

(1) A case of temporary social parasitism. Many observations concerning the mixed colony of *Acanthomyops* (*Dendrolasius*) *fuliginosus* Latr. and *Acanthomyops* (*Chthonolasius*) *mixtus* Nyl. at Bournemouth, which was observed over a period of six years, until the *mixtus* finally died out in 1940, have already been recorded. The proportions when first observed were about 40 *fuliginosus* to one *mixtus* and it was probably already five or six years old, if not more.

Since, therefore, the *fuliginosus* colony was already at least eleven years old when the last *mixtus* worker died, it is clear that the *mixtus* queen was not killed by her own workers, or the *fuliginosus*, or did not die until some years after the entrance of the *fuliginosus* queen. Perhaps in this case of temporary parasitism the queen of the host species is not killed either by the parasitic species, or her own workers, but lives her full life span; only she is not replaced on her death. Certainly this observation seems to point to this hypothesis. Observations made on this colony have already been summarised (Wragge Morley 1944).

(2) A case of phylacobiosis. On 27 April 1944 Dr. Julian Huxley wrote to the author as follows:—"When in West Africa I saw for the first time a number of mushroom-shaped termitaries for shedding rain. On opening half a dozen of these I never saw any soldiers or nasutes, but invariably there was a colony of large black true ants in the termites nests. Could it be that these are symbiotic and take the place of the termite soldiers?"

This is undoubtedly a case of phylacobiosis, a condition first recorded by Wasmann (1901-2) who described such a relationship between the Brazilian *Camponotus termitarius* and *Eutermes fulviceps*. The exact relationship between the ants and the termites was then, as now, not clearly defined, although Wasmann thought that they helped to defend the colony. The apparent absence of the nasutes and soldiers in the case cited by Dr. Julian Huxley seems to indicate that this may be correct. If this be the case, it is an astonishing relationship.

(3) An anomalous case of *Tetramorium caespitum* L. being found in a nest of *Formica rufa* L. In February 1938 the occurrence of a small colony of *Tetramorium caespitum* L. "about 60 or 70 workers—I did not find a female" in the bark of an old tree stump around which a nest of *Formica rufa* L. was built was recorded (Morley 1938). Unfortunately, on being disturbed the *Tetramorium caespitum* left the tree stump so that the exact relationship could not be determined. It is possible that the *T. caespitum* entered the tree trunk while the *F. rufa* were hibernating; otherwise it would appear that this is a case of a hitherto unrecorded host for *F. rufa* during its period of temporary parasitism, or of a plesiobiotic colony becoming xenobiotic.

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OCCURRENCE OF *VANESSA CARDUI* (LEPIDOPTERA) AT SEA OFF THE WEST AFRICAN COAST

By C. B. WILLIAMS, M.A., D.Sc., F.R.E.S.

(Rothamsted Experimental Station, Harpenden.)

IN September 1943 I was on board a ship sailing southwards off the north-west African coast. Butterflies were observed on a number of occasions between the 8th and 15th September as follows.

On the 8th September three were seen flying round the ship from about mid-day (sun time) to 6 p.m. The ship at 5 p.m. was about 160 miles from Cape St. Vincent, Portugal, and about 120 miles from Morocco (see map).

On the 9th September three were seen in the early morning. One male was captured about 8 a.m. and a female about noon. Both were *Vanessa cardui*, the "Painted Lady" Butterfly. The male was very small and pale, the female normal in size and with brighter colouring. The temperature at 11 a.m. was about 77° F.: wind light N.; sea calm; sky cloudless with slight haze. Other butterflies were seen at times during the afternoon and early evening. At mid-day the ship was about sixty miles west of Cape Saffi.

On the 10th September one was seen in the morning and one in the afternoon. The ship in the evening was between the Canary Islands and the mainland.

On the 11th and 12th single specimens were seen each evening flying round the ship.

On the 13th one was seen about sunrise by the Captain, and they were about the ship all morning. Between 8 a.m. and 11.30 four were captured (two males and two females). The weather was sunny through haze; wind fairly strong N.E., following the ship; temperature at 11.30 was 78° F. Other butterflies were seen later in the day. The ship's position at noon was about seventy miles S.W. of Cape Blanco.

On the 14th September butterflies were on board as early as 7.30 a.m. Between 9 and 9.30 six were seen and one caught (a female); all seen were flying low over the water slowly from N.W. to S.E., approximately with a light following wind. The weather was sunny; sea fairly calm but a slight swell from the north; temperature at 10 a.m. was 82° F. Between 9.30 and 10 a.m. two were seen of which one (a female) was captured.

The speed of flight over the water was estimated at 6 m.p.h., so with eight butterflies seen in one hour there must have been about eight butterflies on a six-mile stretch of water on a front of about forty yards. That is, about forty butterflies per square mile of sea, or 300 crossing a mile-front per hour.

One or two were seen "soaring" just a few feet above the water, drifting with the wind for twenty yards or more without fluttering their wings. On the whole they were more active than on the previous day.

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On the 15th September, two butterflies were reported as seen during the morning. In the evening the ship was north-west of Freetown, Sierra Leone, but out of sight of land. The course was then changed and no further butterflies were seen.

Altogether eight butterflies were captured, of which three were males and five females. The distance in a north-south direction from the first seen off

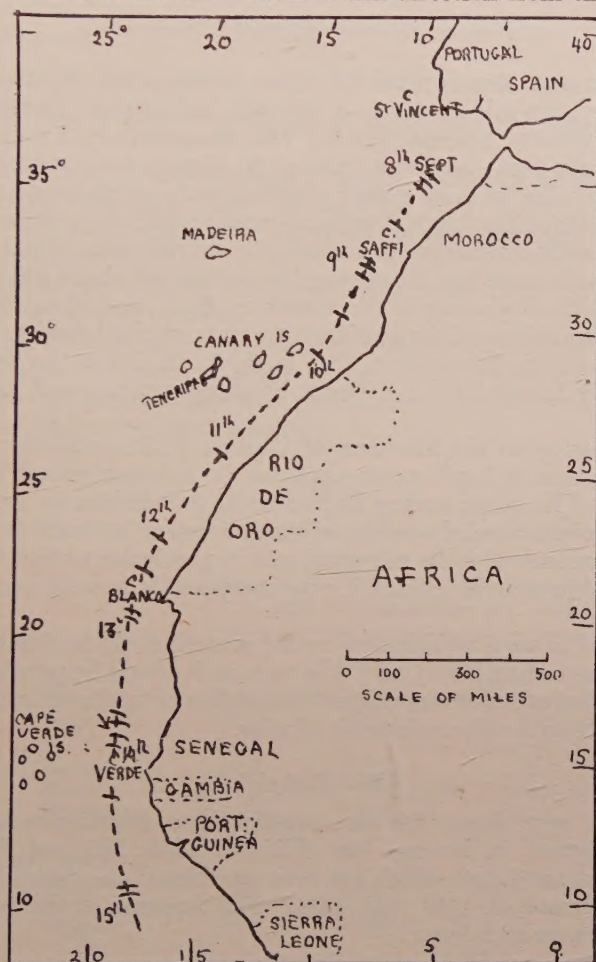


FIG. 1.—Painted Lady butterflies off the African coast in September 1943. Cross lines show approximate position when butterflies were observed.

the Straits of Gibraltar to the last just north of Freetown was over fifteen hundred miles.

It is interesting to note that Stanley (1943, *Entomologist* **76** : 251) records *V. cardui* as abundant round Dakar from the first week in September to the middle of October 1943.

For a discussion of records of abundance of *V. cardui* on the West African coast see Williams, 1942, *Trans. R. ent. Soc. Lond.* **92** : 207. To the list given there should be added a record by Bacot (1916, *Proc. ent. Soc. Lond.* **1916** : v) of large numbers in Freetown, Sierra Leone, in September 1914.

NOTES ON THE FAT CONTENT OF TWO BRITISH MIGRANT MOTHS (LEPIDOPTERA)

By C. B. WILLIAMS, M.A., D.Sc., F.R.E.S.

(Rothamsted Experimental Station, Harpenden.)

IN 1941 Felton and Romney published an investigation of the food reserve stored as chloroform-soluble fat in a migrant leaf-hopper (*Eutettix tenella*) in the States of Utah and Arizona, U.S.A. This insect transmits a virus disease—curly top of sugar beet—and was believed to migrate for distances up to four or five hundred miles from its winter quarters to the sugar-beet areas.

Large numbers of leaf hoppers were collected at different points on the route, and extracted with chloroform to remove the soluble fat. Briefly the results showed that the females had an average fat content of about 40% of their dry body weight at the beginning of the migratory flight, and about 8–10% at the end; with intermediate values at different points on the journey. It was also shown, from the high fat content, that in Southern Idaho the beet fields are almost certainly infected from adjacent breeding grounds and not from long distances.

Recently, owing to the kindness of Captain T. Dannreuther, I obtained very large numbers of Lepidoptera captured in a searchlight at Hastings, on the S.E. Coast of England, during August 1944, and decided to use some of the material to obtain a detailed account of the amount of fat in the bodies of some species that were known to be migrants, and in particular to find the variation from individual to individual, which was not possible in such small insects as JASSIDAE.

I also wished to see if reliable data on fat content could be obtained by using only the abdomen of an insect, as if this were so it would be possible to get the fat content of the bodies of rare migrant butterflies or moths without destroying the specimens from a collector's point of view.

The Material.

Two species were chosen for the investigation; *Plusia gamma* which is a well-known migrant in Europe (see Williams 1930 : 265 and Fisher 1938); and *Phlogophora meticulosa* which has been considered as a possible migrant in the past (Williams *et al.* 1942 : 137, 141). The captures of the two species in the searchlight were as follows :—

	August 1944	<i>P. gamma</i>	<i>P. meticulosa</i>
22–23		5	×
23–24		1920	36
24–25		×	×
25–26		about 5000	230
26–27		about 5500	122
27–28		40	12
28–29		350	130
29–30		4	0
30–31		6	8
31– 1 Sept.		0	0

The sudden appearance and rapid disappearance of both species strongly suggest a migratory flight. The searchlight did not work continuously

after the 1st September. Of the *P. gamma*, a number were selected at random from the specimens captured on the 23-24 August and was found to contain approximately equal numbers of males and females. Two lots of males and two lots of females each of approximately 50 specimens were used for the experiment.

Of the *P. meticulosa*, all the specimens captured on the night of the 26-27th were separated, and were found to consist of 60 females and 62 males. All these were extracted.

Method of Extraction.

The method which was adopted after a few preliminary experiments was as follows :—

(1) The moths were dried for about 2 days in a Calcium Chloride desiccator.

(2) The wings were then broken off and the whole body (abdomen, head, thorax, and legs) was weighed—or alternatively the abdomen was broken off and this was weighed alone.

(3) Each abdomen or body was folded in a small circle of filter paper on which was its registration number.

(4) 25 or 50 of them were put into a Soxhlet fat extraction apparatus and allowed to remain over-night in ether. The following day the apparatus was heated and the siphon circulation was in action for about 6 hours, with a change of ether about once every 15-20 minutes.

TABLE 1.

Plusia gamma summary of results. All weights in milligrams.

			Original dry weight	Weight after extraction	Weight of fat	% of fat
Abdomen only :						
48 Males.	Lowest .	.	15.2	11.9	2.0	13.2
	Mean .	.	28.5±1.03	15.8±0.26	12.6±1.0	44.4 ¹
	Highest .	.	55.6	19.6	38.6	69.4
50 Females.	Lowest .	.	17.5	13.1	3.1	17.7
	Mean .	.	31.5±1.18	17.0±0.35	14.5±1.1	46.0 ¹
	Highest .	.	59.8	25.2	43.4	72.6
Thorax, head and legs :						
48 Males.	Lowest .	.	16.5	15.0	0.0	0.0
	Mean .	.	22.7	19.2	3.4	15.1 ¹
	Highest .	.	27.4	23.1	7.4	27.8
Total body (excl. wings) :						
49 Males.	Lowest .	.	34.5	24.5	6.5	16.5
	Mean .	.	52.5	34.2	18.3±1.1	34.8 ¹
	Highest .	.	73.0	42.0	41.7	60.2
48 Males.	Lowest .	.	33.7	26.9	4.2	11.5
	Mean .	.	51.1	35.1	16.1	31.4 ¹
	Highest .	.	79.6	42.7	42.1	52.9
47 Females.	Lowest .	.	36.5	25.4	1.7	4.1
	Mean .	.	56.6	37.5	19.1±1.8	33.8 ¹
	Highest .	.	98.0	47.5	61.4	62.7

¹ Average obtained from mean weight of fat and mean original weight.

(5) The filter paper packages were then removed from the apparatus, warmed slightly for about 15 minutes to drive off surplus ether, and replaced in the desiccator over-night.

(6) On the following morning the bodies were reweighed. Weighing was done on a spiral spring balance, which was graduated to one-tenth of a milligram, as this was very much more rapid than an ordinary chemical balance. All weights are in milligrams.

The fat was not recovered, but the amount of ether soluble fat was obtained by the difference between the first weight (gross weight) and the second (lean weight).

Results: (1) *Plusia gamma*.

The data obtained are shown in summary in table 1 and in figs. 1, 2, and 3. Full details of all the four hundred weighings are not given, but they can be obtained to the nearest milligram from the diagrams.

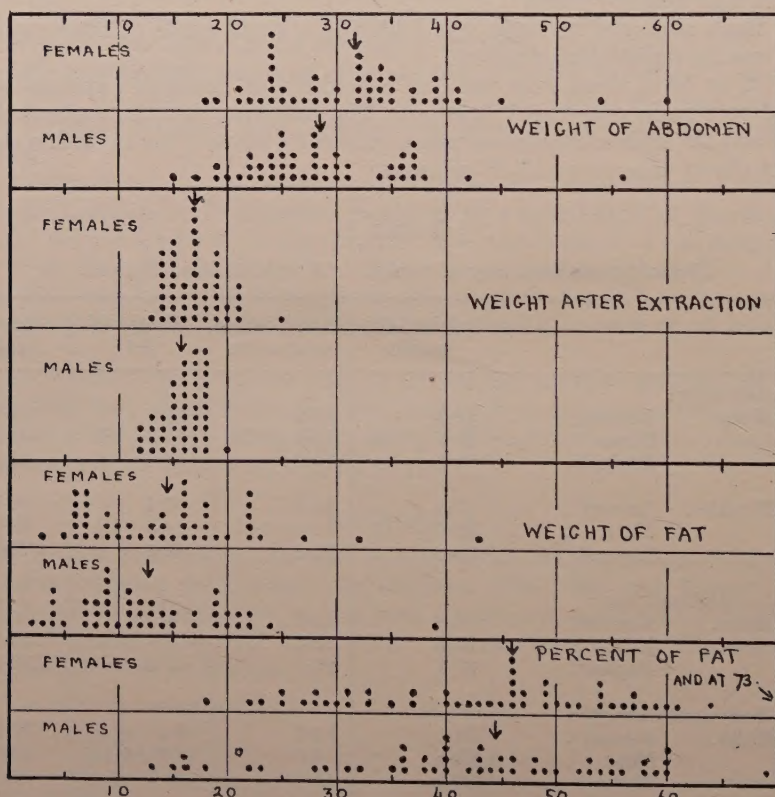


FIG. 1.—Frequency distributions of weights of abdomen of *Plusia gamma* before and after extraction of fat with ether.

Dealing first with the fat content of the abdomen only (fig. 1), it will be seen that the average weight of the abdomen as removed from the dried insect was 28.5 mgs. for 48 males and 31.5 mgs. for 50 females. The variation is, however, very large; from 15.2 to 55.6 mgs. for the males with a standard deviation of ± 7.1 . That is to say, that 33% of the records will be either above

35.6 mgs. or below 21.4 mgs. The variation in the females is of the same order. This indicates that very little reliable information as to the pattern of the whole population can be obtained from a few observations. From the 48 males used in this experiment the average value of 28.5 is only correct to within the limits of ± 1.2 milligrams.

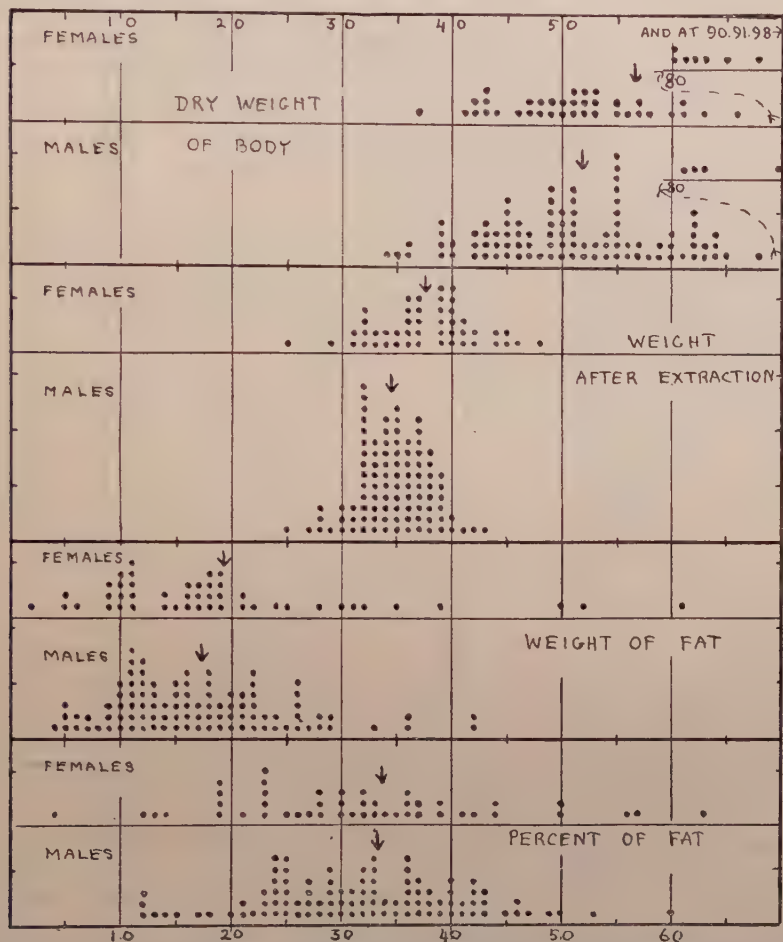


FIG. 2.—Frequency distribution of weight of bodies (excluding wings) of *Plusia gamma* before and after extraction of fat with ether.

The number of specimens necessary for any study depends of course on the degree of accuracy required, and to get double the accuracy it is necessary to have four times as many observations.

After extraction by ether there is a considerable reduction of weight due to loss of fat, and also the new "lean" weights are much less variable than the original dry weights, showing that a large proportion of the variation of original weight was due to fat content. The lean weight of the female abdomens is about 7.5% heavier than the males. The gross dry weight difference was about 10%.

The weight of fat—which is the interesting point in connection with food reserve—is very variable and averages in the males 12.0 ± 1.0 mgs. and in the females 14.5 ± 1.1 . But since the female's lean weight is slightly heavier than that of the male the percentage of fat in the two sexes is almost identical; 46% in the female and 44.4 in the male, the difference being not significant. In the sample of nearly 100 individuals rather less than half the original dry weight

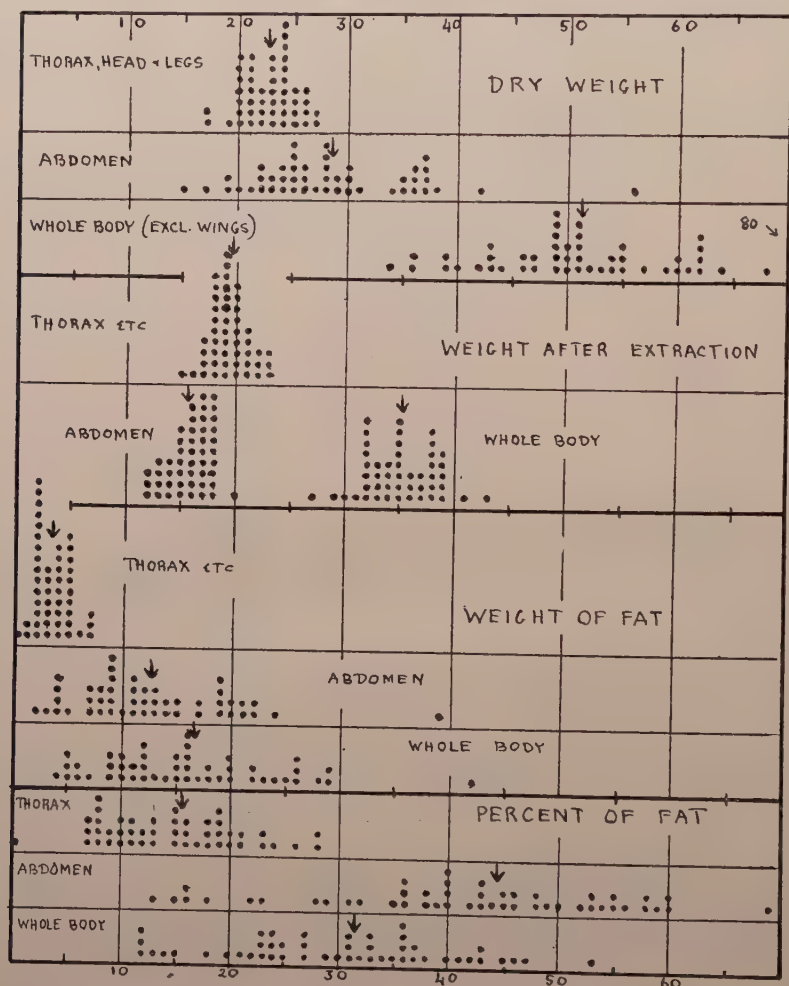


FIG. 3.—Weights of abdomens, of thorax and head and legs, and of whole body of 48 males of *Plusia gamma*, before and after extraction of fat with ether.

of the abdomen was fat soluble in ether—but in different individuals the percentage varied from about 15% to about 70%.

If we take the whole body excluding wings (table 1 and fig. 2) we have for discussion the weighing of 47 females and two sets of 49 and 48 males (fig. 2). The average gross weight of the whole body was approximately 80% more than that of the abdomen alone in both sexes.

The weight of fat is, however, only 30% more, so that the percentage of fat in the whole body is approximately 33% in both sexes with no significant differences between them. The variation is from 4% to 63% in different individuals. The actual weight of fat in different individuals varied from 2 mgs. to 61 mgs. with an average of 19 mgs. of females and 17 mgs. of males. Again the variability is so great that little reliable information could have been obtained from a few specimens.

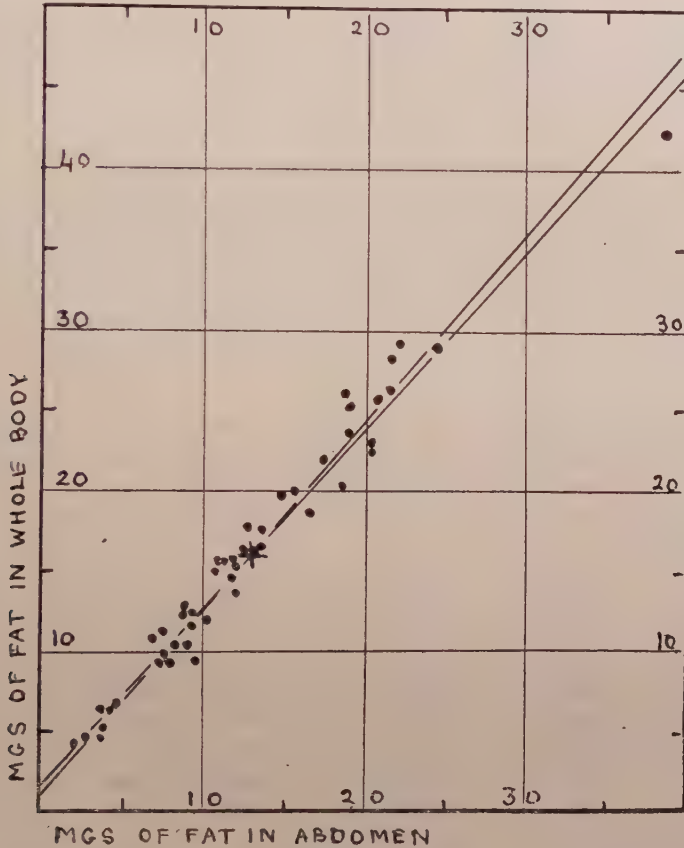


FIG. 4.—Relation between weight of fat in the abdomen and in the whole body, excluding wings of *Plusia gamma* showing a correlation of $+0.98$.

In 48 males the thorax, head and legs were extracted and weighed separately from the abdomens of the same individuals. The average amount of fat in the thorax was 3.4 mgs. as compared with 12.6 mgs. in the abdomens of the same individuals. The gross weight of the thorax was less than that of the abdomen—but after extraction the lean weights were in the reverse order. Fig. 3 shows diagrammatically the frequencies of different weights in the abdomen, the thorax, head and legs and in the two combined (total body) of the same 48 males. There is an average of 15.1% of fat in the thorax, 44.4% in the abdomen and 31.4% in the whole body.

Fig. 4 shows the relation between the amount of fat in the abdomen and the

amount in the whole body of the 48 males. The correlation is very high, ± 0.98 so that information obtained from the abdomen alone gives a very close indication of the fat contents of the whole body. The regression of the fat in the whole body as compared with that in the abdomen only is 1.11—in other words, a change of 1 mg. of fat in the abdomen is on an average associated with a change of 1.11 mgs. in the whole body, one-tenth of the whole change being due to the thorax.

It is interesting to note that in fig. 4 the regression line meets the axis when the amount of fat in the abdomen is nil but the amount in the thorax is about 2 mgs. This may only be accidental, but it accords with the general idea that the abdomen is the main supply of stored energy while part at least of the fat in the thorax is in use and a minimum here is essential.

Results : (2) *Phlogophora meticulosa*.

The results for 62 males and 60 females of *P. meticulosa* are shown in table 2 and fig. 5. In general they confirm the results from *P. gamma* except that there is distinctly less fat in proportion in the abdomen of these *P. meticulosa*.

The average weight of fat in the abdomen of the males is 6.7 ± 1.0 mgs. (*P. gamma* 12.6), and in the females 10.4 ± 1.1 mg. (*P. gamma* 14.5).

TABLE 2.

Phlogophora meticulosa. Summary of results. All weights are milligrams.

		Original dry weight	Weight after extraction	Weight of fat	% of fat
Abdomen only :					
62 Males.	Lowest .	23.3	19.7	1.4	3.8
	Mean .	39.5 ± 1.12	32.8	6.7 ± 0.57	16.9^1
	Highest .	62.9	46.4	20.3	40.0
60 Females.	Lowest .	26.4	22.0	0.8	2.5
	Mean .	46.6 ± 1.47	36.1	10.4 ± 1.13	22.4^1
	Highest .	80.0	46.7	34.2	46.2
Thorax, head and legs :					
62 Males.	Mean .	27.8	24.0	3.8	13.7^1
60 Females.	Mean .	27.9	24.3	3.6	12.6^1
Total body (excl. wings) :					
62 Males.	Mean .	67.8	56.8	10.5	15.6^1
60 Females.	Mean .	74.5	60.4	14.0	18.8^1

¹ Average obtained from mean weight of fat and mean original weight.

In the thorax there is no significant difference in weight between the two sexes. *P. meticulosa* males 3.8, females 3.6 (*P. gamma* males 3.4).

The gross weight and the dry weight of these insects are considerably greater than that of *P. gamma* so that the percentages of fat are considerably lower : 17% in males and 22% in females as compared with 46% and 44% in *P. gamma*.

The range of variability, and hence the standard deviation and probable error of the mean, are of the same order as in *P. gamma*, so that a sample of 60 specimens gives the same approximate degree of accuracy.

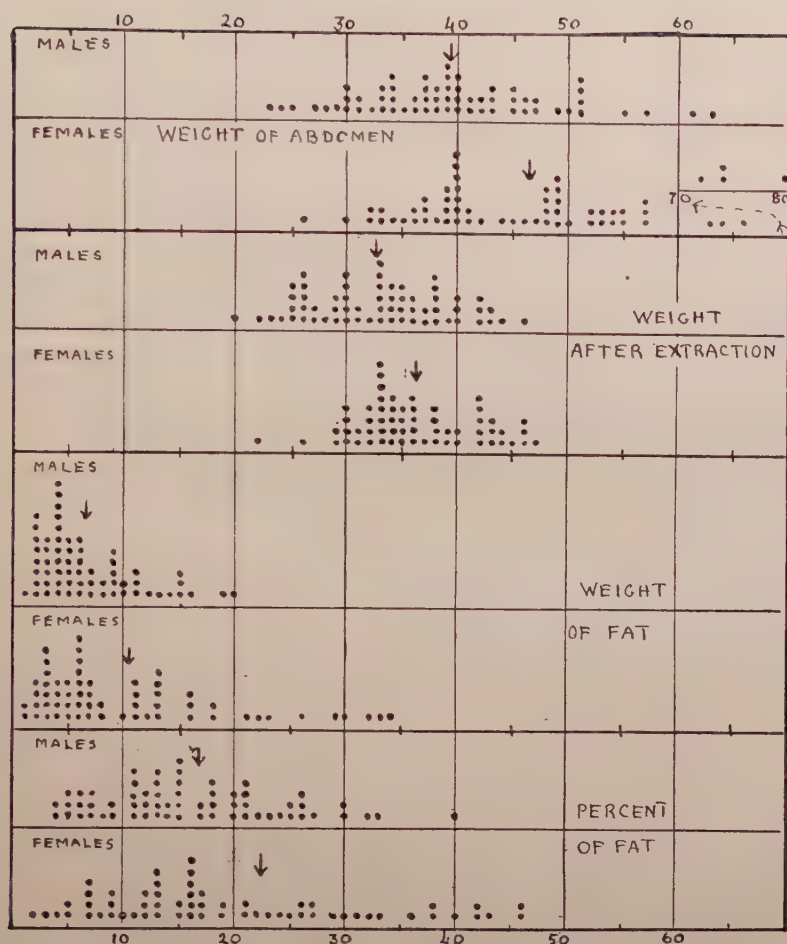


FIG. 5.—Frequency distribution of weights of abdomens of 62 males and 60 females of *Phlogophora meticulosa* before and after extraction of fat with ether.

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"HOW DOES A FLY LAND ON THE CEILING?"

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THE question as to how a fly lands on a ceiling, put to the B.B.C. Brains Trust, has probably provoked more controversy than almost any other question which that body has been called upon to answer. Although the views of many authorities have been publicised, no one has so far provided the complete answer to the question. It has therefore been considered worth while to record the details of an experimental attempt to throw some light on the matter, not because its results are in any way complete or conclusive, but rather because the method used, or a modification of it, may provide a useful starting-point for any more serious attempt to investigate the problem which may be made in the future.

As the aerobatics of the fly in landing on a ceiling are too rapid for the unaided eye to follow, the high-speed cinematograph camera immediately suggests itself as a possible means of recording the significant movements. A photographic record can be studied at leisure by projecting the pictures at a much slower rate than that at which they were recorded so that the eye can follow the movement. Moreover, if the photographs are sufficiently good, individual pictures of the series can be examined for detailed information on the movement (1).

The Eastman Kodak high-speed cine-camera (2) will take photographs at frequencies of up to 3000 per second, and pictures were actually taken at a frequency of 1500 per second, at which rate the 100-ft. length of 16-mm. film passes through the camera in just over 2 seconds.

To increase the chance of a fly alighting in this short time within the 8 in. $\times$ 6 in. field of view of the lens used, some ninety house flies were captured and then released into an enclosed box 12 in. $\times$ 9 in. $\times$ 9 in. in size. The "ceiling" of the box and two sides were made of glass. The camera was arranged with the axis of the 2-in. focal length $f/2$ lens vertical so that part of the glass "ceiling" formed the field of view. This arrangement also had the advantage that it located the fly, as it landed, in a plane which was fixed by the "ceiling" and upon which the lens could be focused. Illumination was provided by four "Photoflood" lamps arranged to illuminate the interior of the box through the glazed "ceiling" and sides. To prevent the flies settling on the floor of the box, two white porcelain photographic dishes with a little water in the bottom were placed so as completely to cover it. These also served as a brightly illuminated uniform background. A little honey and water was smeared on a small area of the surface of the glass "ceiling" to attract the flies and cause them to land within the field of view of the camera lens.

When the flies had been given sufficient time to condition themselves to their environment and to recover from the cramped conditions of the small vessel in which they were kept after capture, they began to fly about inside the box. If they crawled on the sides they could easily be disturbed by striking the side of the box sharply. The technique adopted in photographing the landing

action was to switch on the "Photoflood" lamps, set the camera running, then strike the side of the box, trusting that some of the flies so disturbed would land in the right area during the passage of the film. The "ceiling" was observed during, and immediately after, the exposure of every film to decide whether a fly or flies had actually landed. Only after some fifteen trials did it seem likely that one or two landings might have been made.

The film was processed and then projected at the normal speed of 16 pictures per second, thus giving an effective time magnification of about 100. Only one section was found that looked promising, and repeated projection led to the conclusion that the flies performed a "half roll" in alighting, coming to rest at a slight angle to the direction of flight. The pictures when examined individually in an enlarger revealed rather less than when the series was projected slowly, largely because of lack of definition. The image of the fly was, of course, small, and the detail in the body and legs hardly distinguishable from the graininess of the film. At the picture frequency used, 1500 per second, the exposure time for each picture is about $1/7500$ second. This is not really sufficiently short to prevent degradation in the definition of the wings of the insect, which move very rapidly.

Undoubtedly the technique (3) used here could be much improved should further attempts be made to use a photographic method to investigate the problem. It is obviously even more important that greater attention should be paid to arranging the experimental environment to simulate natural conditions much more closely than has been attempted here. The behaviour of the insect under the experimental conditions described may have been modified considerably by factors such as the limited space, the strong light and warmth from the lamps, and the use of a "ceiling" which was transparent and not opaque.

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STUDIES IN THE GEOGRAPHY OF LEPIDOPTERA¹—II. SWALLOW-TAILS IN DESERTIC S.W. ASIA

By E. P. WILTSHIRE, F.R.E.S.

THIS paper discusses in some detail the range, ecological status and origin in desertic S.W. Asia of *Papilio machaon* L. and *P. demoleus* L., and more briefly the other *Papilio* species known from S.W. Asia.

***Papilio machaon* L.**

Only in one place is *machaon* known to occur outside the Palaearctic Zone and south of the Palaearctic Desert Zone, viz. : in the Yemen Mts. (Lat. 15° N.), at about 7500 ft. Like Abyssinia, these mountains receive a summer monsoon and must be classed as Ethiopian (Tropical). *P. machaon* is usually classified as Euro-Siberian, and is certainly Palaearctic. Other Palaearctic butterflies occurring in the same mountains are *Pontia daphidice* L. and *Lycaena phlaeas* L., both of which zoogeographers classify as Euro-Siberian, though *daphidice* endures desertic conditions better than *phlaeas*. Warnecke's records of *Melitaea didyma* Ochs. from Abyssinia, Yemen and Hadramaut must now be considered to refer to *Melitaea abyssinica* Ob., and its Arabian subspecies *scotti* Higgins (see Higgins (1941) for the specific independence of *abyssinica*). Nevertheless, even if *abyssinica* is not a Palaearctic species, as Warnecke thought, it is a member of a genus which is, in the Old World, otherwise exclusively Palaearctic; Warnecke's deductions therefore regarding its occurrence in Ethiopian territory are still valid.

The southernmost stations of *machaon* at present recorded in entomological literature are :—

Race	Latitude	Height	Place
<i>rathjensi</i> Warnecke	15° N.	7500 ft.	Yemen
<i>saharæ</i> Oberthür	23° N.	? 5000 ft.	Ahaggar Mts.
<i>arabensis</i> Eller	25° 20' N.	425 ft.	Hofuf, Hasa

Warnecke also mentions Baluchistan, Lower Egypt, and Cyrenaica as southerly localities of *machaon*, but these are less remarkable.

It is possible that *machaon* subsp. *arabensis* Eller also inhabits others of the more fertile Arabian oases besides Hofuf; in fact Mrs. V. Dickson, a keen naturalist who has resided for many years at Kuwait and also travelled considerably in E. Arabia, assures me that she has seen *machaon* in Riyadh, and she also thinks she saw it at Qatif, on the coast near Bahrain, though she has never seen it at Kuwait, which is a very waterless locality some distance north of Qatif.

Riyadh lies west of Hofuf at 2250 ft., on Lat. 24° 37' N., thus being more southerly than Hofuf; if confirmed, Riyadh will probably be the southernmost limit of *machaon* in the E. Arabian lowlands; for although considerably higher than Hofuf, Riyadh is hardly high enough to be considered a highland or mountain locality, in the same sense as the Yemen and Ahaggar habitats; at such a southerly latitude, a greater elevation than 2250 ft. would be necessary

¹ No. I in this series appeared in 1944, *Ent. Rec.* 56 : 73-4.

to alter the character of the biotope. In Qatif, Hofuf, and Riyadh alike, if it really inhabits all three, *machaon* will belong to the oasis ecofauna and be strictly stenoeccous.

The occurrence of *machaon* in the lowlands of E. Arabia will be seen to be even more remarkable than at first sight if we consider its range in Persia and Iraq. The explanation may be that the Iraqi race, having its centre of distribution in cooler Asiatic mountains, is hereditarily less fit than the Arabian to endure the climate of the torrid lowlands. The possible explanations offered later of *machaon*'s origin at Hasa will explain equally well its occurrence at Riyadh, etc., if confirmed.

In Iraq and Persia this butterfly does not occur south of about Lat. 33° N. except at considerable heights. In Iraq it was reported from Kut (less than 100 ft.) by Peile and the Bombay Natural History Society, but not from Amarah or Basra, though butterflies had evidently been collected at both.

Having myself resided at Basra in 1942-3 I can confirm its absence in the Shatt-el-Arab delta from my own observations. (In the case of many species of Lepidoptera it would be rash to infer absence from non-observation, but when more than one observant entomologist or collector, over a number of years, fail to detect or capture so conspicuous and familiar a butterfly as *machaon*, the inference may be regarded as fairly safe.) In S.W. Persia, similarly, during my residence at Ahwaz (April-Oct. 1938) I never saw *machaon* there, and on my visits to Bushire (Nov. 1940 and Feb. 1941), both made at likely seasons for *machaon*, I did not see it there. Its occurrence at greater heights, in S.W. Persia, will be described a little later.

Ahwaz and Basra, in the extreme south of the Mesopotamian plain, are, as a matter of fact, deficient in many southward-penetrating species which certainly occur at Bagdad (height, 100 ft.) and probably considerably farther south; among such may be mentioned *Eusphecia pimphlaeformis* Ob., *Pigaera pigra* Hufn., and *Earias irakana* Wils., all three attached to *Populus euphratica*, a tree which grows at Bagdad, Basra and Ahwaz; the absence of *machaon*, therefore, from the extreme south, is neither unique nor surprising and may be ascribed to climatic causes (the heat of the plain at so southerly a latitude); but it makes its occurrence, in splendid isolation in E. Arabia, rather hard to explain.

South-west of Ahwaz, at greater heights, *machaon* occurs as follows:—(a) in Fars, it is common on mountains and in oases at 5000 ft. and higher; neither Brandt nor I found it lower there (Lat. 30° N.); (b) south-east of Shiraz it probably occurs similarly, but perhaps at not less than 6000 ft.; (c) it would not be surprising if it were found to occur at 6000 ft. and higher all along the southern watershed of the plateau (*i.e.* south of Kerman), thus linking up with its known habitats in Baluchistan and the Himalayas. S. Persia lies entirely north of the Tropic of Cancer.

On the west shores of the Persian Gulf, however, there are no high mountains until, just north of the Tropic, the isolated Oman mountains crop out of the Arabian lowlands. The fauna of these mountains is still practically unknown. The Oman mountains extend to the south of the Tropic and there are thought to receive summer rains. The analogy with the Yemen is obvious, and there seems a good possibility that *machaon* occurs in the South Oman mountains. Geologically and perhaps faunistically the Oman mountains are a continuation of the Zagros chain, along which *machaon* occurs farther south than along the Syrian-Palestinian-West Arabian chain. The author does not, however, suggest that a biotope exists in the Oman mountains similar to that of the

S. Zagros; indeed enough is known of the former to warrant a contrary view; what he suggests is that strong Iranian affinities are to be expected underlying a probably highly endemic fauna in S. Oman. This much can be said: that whereas in the S. Zagros there is a characteristic scrub from 2000 ft. upwards of such species as *Prunus*, *Amygdalus* and *Pistacia* (see Wiltshire (1939 and 1941) for details of this), in the N. Oman mountains, the heights are quite bare, and a scrub of *Acacia* and *Prosopis* is found at the foot of the hills. Information is lacking regarding the S. Oman mountain flora.

In Mediterranean climates *machaon* is euryoecous at lower elevations than in Iraq and Persia; the heavier rainfall of Syria, Palestine and Cyrenaica seems to provide the requisite humidity which, in the Mesopotamian plain, is only furnished by an oasis biotope.

But to return to the more desertic territories, which are the chief concern of this paper, and to the desert lowlands, the reaction of *machaon* to this lowland environment in Iraq will now be given in greater detail, and the so-called "migrations" of *machaon* will also be discussed.

At its southernmost stations in Iraq (Kut, Bagdad), the butterfly is restricted to oases; but Peile has published in considerable detail records of its breeding habits on the desert foot-hills between Bagdad and Khaniqin, and I, too, have seen it flying in spring on these foot-hills and others farther north in the plain of Iraq. But neither Peile nor I saw or recorded an autumnal generation on these foot-hills (indeed Peile does not record an autumnal generation from Iraq at all, but I have seen *machaon* in the autumn at Bagdad); Peile's careful accounts of its successive foodplants in the Qizil Robat district show clearly that foodplants on the desert foot-hills are only available in April and May, becoming desiccated or destroyed thereafter: by June the butterfly is obliged to return to an umbellifer growing in irrigation-ditches and along the river-banks, *i.e.* to an oasis environment. Since it is inconceivable that the same species should exhibit two types of phenology in the same locality, and since *machaon* has at least three generations in Iraq, including one autumnal brood, it follows that the desert foot-hills cannot support this butterfly as a permanent resident, and that at this latitude and altitude it resides in the oases, recolonising the foot-hills for one or two generations each spring and early summer. The flatter parts of the desert² it fails to colonise at all.

The phenology of *machaon* varies according to the climate of the habitat; it is potentially successively-brooded. In the butterfly's northernmost, coldest stations, however, there is only one annual generation, and in Britain only a partial second generation. In the more southerly parts of the Palaearctic Zone, on the other hand (*i.e.* Mediterranean, desertic and steppe territories), there are three annual generations at least, and the autumnal generation is a positive criterion of its residential status on a given biotope there. In its one Tropical habitat, the Yemen, Warnecke records *machaon* as flying in June, July, August and October, but does not state whether it flies or does not fly in other months. Probably it does so, but until further records from the Yemen are forthcoming, it is useless speculating about its phenology there. It may, however, be noted that its season of flight in the Yemen, as known at present, is that of the monsoon and the immediately following months.

² The word "desert" is here used for both the "desert" and the "pre-desert" of the French biogeographers. Most, if not all of Iraq, would seem to belong to the second of these two types of ground, and probably *machaon* is unknown in the first even as a temporary colonist. But as it is not yet possible to demarcate the two in the Middle East, the term "desert" is here used in its more popular sense.

In the desert plain or lowlands of Iraq then, even as far north as Lat. 34° N., *machaon* is only able to colonise desert or unirrigated terrain for a short part of the year; farther south, it cannot even do as much as this, and is only found in oases; and south of about Lat. 33° N. it does not occur at all.

The climate and terrain of the Arabian desert is certainly no more favourable to *machaon* than that of Southern Iraq, so the improbability of its having reached Hasa recently across the desert by normal infiltration is apparent. West of Hasa, desert lowlands isolate the oasis where it occurs from the desert highlands of Western Arabia, and the high mountains of Yemen and Assir. *P. machaon* is thus no more likely to have arrived recently at Hasa from the west. Besides, *machaon* is not known anywhere in Western Arabia between Petra, in Southern Transjordan (Lat. 30° N.) where it flies at 4000 ft. (see Graves (1925) and Hemming (1932) for its occurrence there), and the Yemen. It is possible that the high Assir mountains resemble the Yemen mountains and in that case *machaon* may be found in them too, but the Hejaz mountains are presumably not high or well-watered enough for the butterfly.

The Hasa colony of *machaon* is therefore utterly isolated and the butterfly's occurrence there cannot be explained by normal infiltration from some adjacent part of its present range. The remaining possible explanations, which must now be considered, are as follows:—(1) misidentification; (2) mislabelling; (3) chance importation by a collector, followed by (a) extinction, (b) survival; (4) importation on foodplant, followed by (a) extinction, (b) survival; (5) immigration followed by (a) extinction, (b) survival; (6) survival of colony from an earlier age when climatic conditions were different.

For obvious reasons, (1), (2) and (3) can be ruled out. Explanation no. 4, however, raises a possibility in dismissing which one can be less positive. This much can be said:—if the foodplant of *machaon* at Hofuf is like that at other places in S.W. Asia, viz.: *Ruta* and Umbelliferae, it is most improbable that such plants can have been imported to Hofuf, Hasa. It is true that potted plants of *Ruta* are on sale at Bagdad and there occasionally attract *machaon*; but a large potted *Ruta*, capable of attracting ovipositing females or carrying larvae or pupae, would be too fragile to survive so long and rough a journey, nor would such an importation be profitable enough to make it worth the while of a resident of Hasa to try it. But the importation of *Citrus* trees is not out of the question, and since there are records of *machaon* feeding on *Citrus*, this possibility cannot be dismissed positively until the foodplant of the butterfly at Hofuf is recorded, but may be classed as remote in view of the known foodplants of the butterfly in its next nearest habitats and the known presence of at least one Umbellifer species at Hofuf.

Until the foodplant of *machaon* at Hofuf is known, speculation as to the origin of the butterfly there is naturally impeded; if we exclude the possibility of *Citrus*, for the reasons already given, only one possible foodplant remains on the list, given by Cheesman, of Hofuf's flora. I refer to the plant he describes as cultivated Aniseed, *Anethum graveolens* L., "grown in most gardens," "in flower in November."

Unfortunately this determination apparently cannot be unreservedly accepted, for Dr. Zohary, the botanist of the Hebrew University, Jerusalem, whom I consulted as to the possibility of this plant being indigenous at Hofuf, and also as to the possible method of its being introduced thither, replied that *Anethum graveolens* was well known in Palestine and Syria, being a cultivated annual, was propagated only by seeds, and escaped readily into fallow fields, but could not be indigenous at Hofuf; he went on to say that from the statement

that it flowered in November at Hofuf a doubt arose as to the correctness of the determination, for "*Anethum* flowers exclusively in spring."

It will thus be apparent that if Cheesman's aniseed was correctly determined, it must have been introduced into Hofuf in the form of seed, and consequently *machaon* could hardly have been "introduced with the foodplant" by human agency; and if the Hofuf aniseed was in fact some other species of Umbellifer, the probability is no greater.

Alternative (a) under explanations nos. 3, 4, and 5, will be ruled out if and when a second traveller brings back specimens of *machaon* caught at Hofuf in a different year; but I am inclined to accept Mrs. Dickson's record of the species in Eastern Arabia, though she brought back no specimens, as sufficient proof that Cheesman's capture of it there was not due to a unique coincidence of collector and prey.

Explanation no. 5 (immigration, in the sense of C. B. Williams) may at first sight seem attractive, but on closer examination will be found improbable, to say the least. It is true that well-known migrants such as *Vanessa cardui* L., *Macroglossum stellatarum* L., and *Celerio lineata livornica* F., migrate northwards from Arabia into Iraq and the mountains of Persia and Kurdistan every summer, presumably returning, less conspicuously, every autumn (cf. Williams, 1942, on the return flight). In Iraq, however, as has been shown, *machaon*'s migrations are comparatively short and local; nowhere in Europe has *machaon* been cited as a migrant³; only in India (see Williams 1938) has it been mentioned as migrating, and there on the strength of a single observation by Peile. Migrations of *machaon* in the Himalayas, if they truly occur, would be very relevant to this discussion, and would simplify the explanation of the origin of the Hasa colony, but the record of "several" individuals moving "from North to South against the wind" on one day at 7000 ft. in the Himalayas is not proof of any considerable migratory tendency in this species. Granted that there are all intermediate grades between complete stability of residence and the most extensive migrations, and that *machaon* is not an absolutely stable species, there is nevertheless no evidence warranting the supposition that migration helps it to penetrate the Palaearctic Desert Zone. If it can migrate to Hasa, why has it never been observed at Basra and Bushire?

The only remaining explanation, therefore, is that *machaon* has survived intact at Hofuf, Hasa, from a previous age. Even this hypothesis, it must be admitted, presents difficulties, and the following suggestions are offered for what they are worth.

Possible Explanations of the Occurrence of P. machaon at Hasa.

The Hasa oases (Hofuf and Mubarratz) differ from neighbouring E. Arabian wells and oases in the great number and copiousness of their springs, hot and cold, which irrigate extensive flourishing palm-gardens and support a population of at least 50,000 souls.

All authorities agree that the desiccation of Arabia is geologically recent, that the process is continuing in the same direction, and that rivers once flowed where now are arid *wadis* or shifting sand-dunes. Local lore and geological evidence both support this view. On the exact recency of the desiccation, there is of course less unanimity. Philby concludes: "The rivers of the great

³ Cf. Morley 1943, regarding Continental *machaon* sometimes reaching Britain; the author rightly describes such arrivals as "sporadically wafted from abroad," a description inapplicable to the immigrations of *V. cardui* L., *C. crocea* Fourc., etc.

desert would at any rate seem to have flowed until the very dawn of history, if not within historic times." The more recent their disappearance, the easier will it be to explain the continued existence of *machaon* at Hasa. During the Pleistocene Pluvial periods Arabia was certainly less desertic than now; then, if not later, the lost rivers of Arabia undoubtedly flowed, from sources in the western highlands, to their mouths in the Persian Gulf, which then extended farther northwards than it does now.

These rivers can be traced in the Widian valleys west of Kerbela, flowing N.E. into the Euphrates basin; the Batin, flowing N.E. to Basra, or rather to Zubeir, for Basra was then under the sea; the Wadi Hanifa, flowing by Riyadh and not far from Hofuf; the Wadi Sahba; and the Wadi Dawasir, flowing eastward into the Empty Quarter.

At some period when the climate of Arabia was less arid, a number of Palaearctic species spread southwards along the high mountains of Western Arabia as far as the Yemen; six of them penetrated East Africa and still survive there at a high altitude (see Warnecke 1933) but *machaon* was not among these six. The straits of Bab-el-Mandeb were no obstacle to this invasion, for, as Uvarov, summarising Blankenhorn and Krenkel, remarks, "The Red Sea rift was formed in Eocene-Oligocene times but throughout the early Tertiary it was not invaded by the sea and contained some freshwater lakes. . . . It was not until the beginning of the Pleistocene that the waters of the Indian Ocean filled up the rift from the Gulf of Aden to the Gulf of Suez."

We may suppose then that *Pontia daphidice* and *Lycaena phlaeas* and the other four species referred to in the previous paragraph invaded Africa via West Arabia and the Yemen along high ground before the early Pleistocene.

Later, during one of the Pleistocene Pluvial periods, *machaon* followed the same southward course, but, the straits now existing, penetrated no farther than the Yemen highlands.

The above is a reasonably safe inference from the known range of the species in question and our geological data. What follows would be more speculative, if not confirmed by taxonomic evidence.

The more humid climate of Arabia during the above period (preferably the most recent of the Pluvial periods) also provided a biotope which enabled *machaon* to spread from the western Arabian highlands eastwards towards the Persian Gulf, this biotope being a riverain flora; the butterfly thus reached Hofuf and probably other places in E. Arabia. But when Arabia was again desiccated, *machaon* died out in all its Arabian habitats except two exceptional localities:—the Yemen mountains, where the rainfall and height favoured its survival, and Hofuf where the abundant water and vegetation did likewise.

The reported survival of *machaon* at Riyadh, if confirmed, will strengthen this hypothesis of a western origin for the butterfly's Hofuf colony, for Riyadh marks the route probably taken by *machaon* on its eastward journey from the heights of Western Arabia, being a point on an ancient river-bed, where, as at Hofuf, copious water is still to be found.

The above hypothesis finds strong support from the taxonomic evidence. Eller (1939), who analysed all known subspecies of *machaon*, has quite definitely stated that the two Arabian races, *rathjensi* and *arabensis*, are morphologically and anatomically (genitalia) more closely related to the Mediterranean group of subspecies than to the Asiatic one. According to him, the Arabian races have undoubtedly been derived from the Mediterranean ones and not from the Armeno-Persian, as might have been expected from the present geographical

distribution. It is interesting that the hypothesis of a western origin, based on ecological and geographical grounds, was formulated before Eller's opinion, based on structural grounds, was known to the author.

***Papilio demoleus* L.**

This butterfly finds in Arabia its westernmost limit; it is a tropical (Indo-Malayan) species and a well-known migrant in India and other Oriental tropical lands.

Migrations of *demoleus*, however, have never been reported in S.W. Asia, and it is noteworthy that while inhabiting S.W. Persia slightly north of Lat. 30° N., it is yet entirely absent from Iraq. I have personally found it at 3000 ft. (Kazeroon plain) and 5000 ft. (Shiraz) in S.W. Persia, and have found its larvae there feeding on *Citrus* foliage and apparently a stable resident, common in suitable oases.

Among a consignment of Rhopalocera taken by Mr. D. Vesey-Fitzgerald in April 1943 in the neighbourhood of Sharjah (North Oman) and sent to me for determination, was a specimen of *demoleus*. The sender had found it common in date gardens there; those gardens undoubtedly also contained lime-trees.

Since Cheesman took *demoleus* at Hofuf, and it is also known from Muscat (S.E. Oman), the Sharjah record is not surprising; the Hofuf record remains the north-westernmost known limit of the butterfly, though more southerly than some of its Persian habitats.

The extreme westernmost locality seems to be the Wadi Dawasir, in S.W. Nejd; this is 400 miles south-west of Hofuf. (A single male taken by H. St. J. Philby on 15.iii.1932 at Suleiyal, Wadi Dawasir, is in the British Museum.)

The question how *demoleus* reached Arabia is naturally bound up with the question how its foodplant reached there. The following quotations regarding *Citrus* origins are from Sir George Watt (1908) *The commercial products of India*:—

“The different forms of the orange, the lemon, the citron, the lime and the pomelo constitute a tropical assemblage of fruits. . . .

“While the orange (*Citrus aurantium* L.) is indigenous to China, and the limes to India, the citron originated possibly in Persia and Media, while the lemon is so closely associated with the Arabs as to suggest its having come from Arabia. The Arabs, at all events, carried its cultivation to Africa, Egypt and Europe. In the tenth century, for example, we read of them conveying it from the gardens of Oman to Palestine and Egypt. The earliest Arab and Persian writers who knew of the citron and lemon are Serapion and Rhases, who describe the former, while the latter is alluded to by Ibn Baithar. Avicenna, the author most frequently cited, apparently confused these plants.”

“*Citrus decumana* L. Pomelo. A native of the Malay Archipelago.

“*Citrus medica* L. (a) *medica*. The Citron, said to have been found wild in Chittagong; by others reported as wild in the Khasia and Garo hills and also in Kumaon.” (N.B. Not reported wild in Persia or Media.—E.P.W.)

“(b) *acidum*. Sour Lime. The plant usually met with in a wild state in the warm valleys of the Himalaya. The wild lime is in fact the chief budding stock for all species of orange, lemon, and citron.

“(c) var. *limetta*. Sweet Lime. Wight regarded the Sweet Lime as indigenous in the Nilgiri Hills.”

Since Sir George Watt reports three varieties of the species *medica* as indigenous in India, and as there is no botanical evidence of any of the four forms of this species occurring wild in Persia or Arabia, it seems questionable whether his tentative attribution of the citron to Persia and the lemon to Arabia, on the grounds of historical association, is tenable. It must, however, be admitted that these two trees, the citron and lemon (*C. medica* and *C. medica* var. *limonum*) could only have thrived originally in Persia and Arabia in natural oases; that while in Persia the flora of natural oases, which can still be observed owing to that country's greater water-supply, appears never to have contained these trees, it is hard to know what the original flora of Arabian natural oases was, so completely have the Arabian oases been cultivated and transformed in the course of history.

Of *demoleus* it can therefore be said that unless a *Citrus* is indigenous in Arabia (the most likely place would be S.E. Oman), and there is no botanical evidence that such is the case, the butterfly cannot have reached Arabia and survived until man brought its foodplant there; and that it probably became established, with lemon as its foodplant, in Muscat, before the 10th century A.D. The butterfly's arrival in the other *Citrus* gardens of S. Persia and Arabia may have taken place by immigration, by importation with foodplant, or by both of these alternatives.

At first the second alternative may appear unnecessary, but there are some objections to supposing that immigration alone is responsible for the present occurrence of *demoleus* in these gardens. The first is the apparent lack of the migratory impulse in *demoleus* in these regions, and the second is that *demoleus* has not gone farther, *i.e.* to Iraq, Africa, and the Mediterranean. For if *Citrus*-gardens at 5000 ft. (Shiraz) in Persia are climatically suitable for *demoleus*, so are the lime gardens at sea-level in the extreme south of Iraq, for they are on the same parallel of latitude and certainly no colder; and if their rainfall is less than that of the Shiraz district it is certainly more than that of the Hofuf and N. Oman habitats of *demoleus*. Therefore, if the migratory tendency still existed in this butterfly in S.W. Asia, one would expect to find it in Iraq. No migration has, in fact, been reported of this butterfly west of India.

Should *demoleus* in the future reach Iraq in some way, it might well establish itself there; such an event might either occur by importation with the foodplant, or would be evidence that the migratory tendency still persists in S.W. Asia. At present, however, the evidence suggests that this butterfly does not migrate in these parts. How then did it reach its present outposts in Arabia and Persia? By importation with the foodplant, or perhaps in early historical times before the extinction of the migratory tendency? One of these two alternatives must be chosen.

As in the case of *machaon* (above), so also in this case I would be reluctant to suppose a butterfly to have been more migratory in the past than the present, but *demoleus* is still a very active migrant over most of its range, which cannot be said of *machaon*. There is thus less objection to supposing that several thousand years ago *demoleus* was more migratory in the S. Persian and Persian Gulf region than today, especially since the climate of those parts may have been then more humid; indeed, if those regions were then directly subject to a monsoon, as most of India is today, ecological analogy would demand that we consider *demoleus* to have been then as migratory there as in India now. Furthermore, since in early times the waters of the Gulf covered much of the Iraqi plane, we can suppose that the migratory habit died out, with the gradually changing climate, before the coast-line and lime-cultivation of Iraq

reached its present southernmost extent, and use this supposition as an explanation of the butterfly's absence from Mesopotamia.

On the other hand, the alternative of importation by human agency is probably preferable to the above as being less speculative; if we adopt this alternative we need not presume the dying out of a once active migratory habit, but merely the weakening of the habit at the fringes of the butterfly's range, where it has been imported and where there are certain climatic obstacles (aridity, and colder winters) not found in its centre of distribution. To the possible objection that importation has not enabled *demoleus* to establish itself with imported *Citrus* elsewhere in the world, *e.g.* Africa, the Mediterranean, the West Indies, and California, it can be answered that the distance covered and the time taken by importations to these regions would doubtless be fatal to any of the early stages of a successively-brooded insect like *demoleus* attached to a cutting exported from the butterfly's centre of distribution, whereas the sea-journey from India to the Persian Gulf would not necessarily be fatal to *demoleus*.

The least unlikely histories of the Arabian colonies of *machaon* and *demoleus* in my opinion are therefore as follows :—

	<i>machaon</i>	<i>demoleus</i>
Direction of arrival . . .	from Palestine via Western Arabia.	from India via S. Persia and Muscat.
Means of travel . . .	infiltration by its own powers of flight.	importation by man on foodplant.
Time of arrival . . .	Pleistocene Pluvial Period.	Historical times.

Other *Papilio* species of S.W. Asia.

(1) *Papilio demodocus* Esp.

The author has no personal experience of this butterfly in a state of nature; it is only found in Asia in S.W. Arabia. Scott records it as common on "bare stony knolls on Jebel Jihaf and elsewhere," *i.e.* it inhabits the Aden Protectorate and the Yemen, frequenting mountains. There is also a specimen at Tring received by the British Museum from Mr. A. C. Trott, who took it 40 miles north-east of Jeddah on 5 April 1940, on the summit of the mountain Jebel Sidir (2000 ft.). This is interesting for two reasons :—it is the northernmost known limit of the butterfly in Asia (though still south of the Tropic), and it is a locality without any monsoon rains. The butterfly illustrates the strong Ethiopian character of S.W. (Tropical) Arabia, and has apparently crossed the track of *machaon*, both species having used the west Arabian mountains to extend their range.

(2) *Papilio alexanor* Esp.

This is confined to high mountains well north of the Tropic, *i.e.* the Lebanon and Zagros ranges; along the latter it extends to the Shiraz district (Lat. 30° N.), flying there at 8000 ft. and higher. It is never common in its Middle East haunts. It also inhabits the mountains of Southern Europe.

(3) *Papilio (Iphiclides) podalirius* L.

This Euro-Siberian species inhabits mountains in S.W. Asia, occurring at lower elevations in the Lebanon than at corresponding latitudes in Iraq and Persia, doubtless because of the more humid climate of the Lebanon. South of Lat. 33° N. it is not known at all, though suitable foodplants exist south of

that parallel. In Iraq and Persia it flies at 4000 ft. and higher, and in the unwooded parts of Persia inhabits oases.

In conclusion, the author wishes gratefully to acknowledge the assistance Capt. N. D. Riley and Dr. E. A. Cockayne have given him by referring, on his behalf, to specimens and literature.

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NOTES ON THE ECONOMY OF THE ROSE-GALLS FORMED BY *RHODITES* (HYMENOPTERA, CYNIPIDAE)¹

By K. G. BLAIR, D.Sc., F.R.E.S.

MUCH has been written on the rose-galls formed by the flies of the genus *Rhodites*, of their incidence on the different species of *Rosa*, of the scarcity of the males of some of them, and of the small numbers of the gall-flies that are reared from them compared with the hosts of inquiline and parasites. Numerous lists of these inquilines and parasites have been published, but so far as I know, though my knowledge of the literature of the Hymenoptera is very deficient, little has been done in the way of working out the association of the various species with one another. I have recently published an epitome of my own experience in rearing from galls of *R. rosae* (1943, 1944), and have established the parasitism of the Ichneumonid *Orthopelma luteolator* Ratz. as an internal parasite upon the *Rhodites*, and of *Torymus bedeguaris* L. and *Oligosthenus stigma* F. as external parasites on the same; of the *Oligosthenus* and of *Eurytoma rosae* Nees on the inquiline *Periclistus brandtii* Er.; and the hyperparasitism of *Habrocytus bedeguaris* Thoms. on all these parasites except perhaps the *Eurytoma*, which usually escapes too early from the gall.

To the parasites there listed may be added *Torymus auratus* Fourc., smaller and greener than *T. bedeguaris*, with an ovipositor scarcely as long as the abdomen instead of as long as the whole body. It would appear to be a parasite of the *Periclistus* as it has been reared from galls composed entirely of these cells.

In an effort to determine the function of each species in the gall, the procedure was adopted of opening the cells between autumn and spring when the larvae of most of the species concerned are full grown and lying in a prepupal state awaiting pupation shortly before the flies are due to emerge. The different species of larvae are then segregated and in due course the majority of them mature without further trouble. The mortality by this method is, I think, very much less than if the flies are left to emerge from the unopened galls, in which the number of flies that fail to achieve their exit from the dried and hard galls is very considerable, while the information that is to be obtained as to their life history is of course vastly greater. This mortality is naturally less when the galls are opened in the spring than when the larvae have been exposed all the winter, but early opening, even before the larvae have reached their full growth, affords yet further information, though of course, as these larvae are almost certain to perish, one has to be able to recognise the different species in this stage in order to know exactly what one is dealing with. As means for identifying these various larvae are not readily available the following notes on such larvae as I have been able to identify may be helpful.

The Bedeguar gall (*Rhodites rosae* L.).

The *Rhodites* larva is stout, tapering strongly towards the tail and less so towards the head, sharply bent on the underside at the base of the abdomen, the intersegmental constrictions deep, and the last segment nearly cylindrical,

¹ See 1943, *Proc. R. ent. Soc. Lond.* (C) 8:36.

about as long as thick or a little longer; colour whitish tinged with yellow, especially the abdomen; the body is hairless, the head not very much smaller than the prothorax and the jaws stout, heavily chitinated, with three teeth along the inner edge; these edges nearly meet when at rest and the tips slightly overlap. Before winter the larva contracts very considerably, the tail becoming somewhat reflexed dorsally. As with most of these larvae, pupation takes place in the spring, about May.

Periclistus brandtii Er., its common inquiline, is not always present. Its cells are smaller than those of the *Rhodites*, more irregular in shape, and often fused together to form a solid mass. I have not observed their actual origin in this gall, but from the fact that one may often discern a grouped arrangement in spherical masses, one may assume that development follows much the same course as it does in the unilocular galls of *R. eglanteriae* Htg., the smooth pea-gall. If one of these galls be opened when still soft and green, about mid-August, the central chamber will be found to have a diameter about equal to the thickness of its wall, beautifully even and lined with large shining green cells. Lying on this wall may be seen a number of elongate, clear, almost colourless eggs, each with a stalk at one end about as long as the egg itself. The stalk appears to be attached to the wall at its other end and to be to some extent elastic, so that if an attempt be made to pick up an egg on a brush it is at once pulled back again. In another gall these eggs were found to have hatched, and were replaced by delicate clear colourless larvae with large knobbly-looking heads which they repeatedly jerked up and down. In yet another gall each of these larvae was found to be sunk in a deep pit in the wall of the gall. They were too small to have eaten out this pit; it appeared as if the wall of the gall had grown inwards between the larvae, but that this growth had been inhibited in the immediate vicinity of the larvae, perhaps by the head movements already noted. It is well known that an inquiline gall grows considerably larger than one not so infested, and it seems that this same stimulation to growth results in the inward growth that forms the pits containing the *Periclistus* larvae, and eventually closes them, at the same time reducing the central chamber. The fate of the *Rhodites* egg or young larva that had presumably originally occupied this chamber was not ascertained, but no *Rhodites* larva was found in any chamber that had been reduced by this development of the *Periclistus* cells. When full grown the *Periclistus* larva is stout and hairless, not much tapering at either end, the intersegmental divisions not so marked as in *Rhodites*, and the tail end is bluntly rounded, with no terminal narrow segment. At each side of each thoracic segment is a slight dorso-lateral swelling, which makes the dorsum appear rather flattened. The jaws are stout, strongly chitinated with the apex more produced than in *Rhodites* but the teeth less developed.

Orthopelma luteolator Gr. This is an internal parasite of the larva of the *Rhodites*. When fully fed it leaves the host larva and is then sausage-shaped, i.e. slightly curved, of even thickness throughout and bluntly rounded at each end, the segmental divisions not deeply incised and with a lateral beading along the sides of the abdomen. The head is not much smaller than the prothorax, the jaws but feebly chitinated, long, slender, arcuate, with the tips slightly overlapping when at rest; the body surface is glabrous and shining. It feeds as an internal parasite, giving no external sign of its presence until full grown, about the end of September. By then it has absorbed the entire body contents of its host, to which it imparts its own shape, though the jaws of the host of course remain in position. The body, however, is dull, and the skin is drawn

into clinging wrinkles in various directions so as to give it the appearance of being an extremely bad fit. On the underside of the prothorax, beneath the skin, can be seen the characteristic jaws of the *Orthopelma* larva. After a few days at most, it casts off this skin and reveals its true form. In a few weeks, towards the end of October, it begins to develop a waist, the thoracic segments becoming more compact and the first two abdominal more slender. At the same time the large compound eyes of the adult commence to colour up within the prothorax, and these developments are more pronounced in the spring, about April, before pupation takes place. This description, it will be noticed, is utterly at variance with that given by Morley (1907), and indeed the only larva in the gall that accords with Morley's description is that of the *Rhodites* itself. Morley may well indeed have reared the *Orthopelma* from the larva he describes, but it is strange that he should not have observed all the intervening stages outlined above. He actually comments upon the great difference in form between his supposed larva of *Orthopelma* and the pupa, almost as though he had an unacknowledged suspicion that all was not as it should be. He evidently failed to recognise the identity of his larva with the more contracted prepupal condition in which it passes the winter and with which he must have been familiar. In my own investigations a number of larvae set aside in the autumn as those of *Rhodites* and not examined until the following April were then found to be for the most part larvae of *Orthopelma*.

Torymus bedeguaris L. Larva white, clothed with erect hairs, long and soft on sides and venter, short on the dorsum; body thickest at first three or four abdominal segments, thence rapidly narrowing to the tail; segmental divisions well marked but not very deep, a median dorsal prominence at base of first two abdominal segments; skin studded with low rugae. Head rather prominent, feebly transverse, more than half as wide as the first thoracic segment, frons evenly convex. Jaws slender, curved, sharply pointed, without teeth, slightly overlapping at apex, not heavily chitinated.

Torymus auratus Fourc. The larvae of this species have not yet been observed, but the fact that the fly has been reared from galls apparently composed entirely of the cells of *Periclistus* makes it tolerably certain that this species is the host.

Oligosthenus stigma F. An ectoparasite on both *Periclistus* and *Rhodites*. The full-grown larva is white, tapering strongly towards the tail and much less so towards the head, segmental divisions not deeply constricted; a median dorsal protuberance on the posterior border of each of the first four abdominal segments. Body curved like a ?, i.e. the under surface not sharply angulate as in *Rhodites*; greatest thickness about 2nd and 3rd abdominal segments; clothed with long soft hairs curved outwardly and ventrally. Head transversely cordiform, twice as wide as long, the frons depressed in the middle, with two deep elongate brown fossae, which nearly meet above. At an earlier stage these fossae are not strongly coloured, and so less obvious. Jaws slender, curved, with a sharp tooth on inner side some distance before apex.

Eurytoma rosae Nees. I was unable in the spring to find any larva in the galls of *R. rosae* that I could attribute to this species, but found a single fly ready to emerge in a gall that, when found, in May, had several exit holes in it. It contained, however, a number of living larvae of various kinds and subsequently produced flies of *Periclistus*, *Oligosthenus* and *Habroclytus*, and appeared to be composed entirely of *Periclistus* cells. But when fresh galls of *R. eglanteriae* were collected in August flies of what appears to be the same species of *Eurytoma* emerged within a day or two. On opening a gall from which a fly had emerged,

it was found to be unilocular, but the cavity, instead of being left empty and tidy, with walls reduced to an even thinness, as is usual with *Rhodites*, was loosely filled with scraps of dry frass and the walls were very uneven in thickness; in some places quite thick, in others excavated nearly to the surface. Similar galls that had not yet produced a fly exhibited the same state of things, the space being still occupied by the *Eurytoma* larva lying amongst this frass. Working backwards, as described for the *Periclistus*, the following course of development was pieced together. Galls containing the eggs of *Periclistus* often contained a few, perhaps four to six, eggs of a different kind, with a somewhat infuscate tougher shell, and without stalk, sometimes singly, sometimes heaped two or more together. Later the larvae were found on the inner wall of the chamber, at the same time as the *Periclistus* larvae, but they were not seen to attack them. Later still, when the *Periclistus* larvae were sunk in the pits, these other larvae were observed entering the pits and devouring the *Periclistus* larvae, and as the pits became closed in they were found tearing down the walls to get at the occupants and even biting a way from one cell to another. It thus appears that they are active predators upon the *Periclistus* larvae rather than parasites, and thus develop very much more quickly than their hosts, the fly in some cases emerging before the hosts were even full grown. Not all of them go straight through to the adult in this manner, but a considerable proportion remain as full-grown larvae, hibernating in this stage and emerging a little before the other inmates of the gall. (It is possible that two species of *Eurytoma* are involved.) Though as already stated, several of the young *Eurytoma* larvae may be found in a single gall, yet only one appears to reach maturity. The presence of the *Eurytoma* among the *Periclistus* and its destruction of the gall-tissue naturally interferes with the normal growth of the gall that results from presence of the *Periclistus* alone. So the *Eurytoma* usually emerges from galls not or but little larger than uninquilined galls,² and I have not found it in large galls containing a good number (15 or so) of *Periclistus* cells, though it does not always destroy all the *Periclistus*. This habit of the *Eurytoma* larvae of preying actively upon the *Periclistus* larvae, one after another, is unusual for a Chalcid, and its biting away of the gall tissue is of interest when we remember that the closely allied genus *Isosoma* (*Harmolita*) is habitually vegetarian, forming galls on various grasses, and is itself parasitised by its near relative *Eurytoma*. Most of the genus are parasitic on gall makers, Dipterous and Coleopterous as well as Hymenopterous, and it is possible that we have here an indication of transition from a vegetarian gall-feeding or inquiline habit to the more nourishing diet provided by the gall-makers themselves. I do not know, however, whether this active predatory habit is found in any other of the species.

The larva of *Eurytoma rosae* is white, moderately slender, thickest about the second abdominal segment, thence tapering towards each end. There is a transverse median dorsal process at the base of the third thoracic segment and of the first seven abdominal segments and a lateral beading on abdominal segments 1-6 immediately above the tracheal trunk. There are a few long curved hairs on the head and prothorax, elsewhere with sparse short hairs. Head transversely cordiform. Jaws well chitinised, rather slender, with a long curved tip, which overlaps its fellow when at rest, and a sharp tooth on the inner side some distance behind it.

Habrocytus bedeguaris Thoms. These larvae I have found only in late

² A small or moderate-sized gall with *Periclistus* cells when cut into is hard and much more resistant to the knife than one not so infested.

spring, closely applied to the prepupal larva or pupa of one of the parasitic species, most often perhaps of the *Orthopelma*. It seems to feed up fairly rapidly, as small and full-grown larvae and pupae may all be found at the same time, though not usually in the same cell, except that the larva has been found attacking the pupa of its own species. The host larva or pupa is not completely consumed. How these larvae obtain access to the cells has not been ascertained, though possibly the eggs are deposited in the autumn, before the gall tissues have hardened, and development is delayed until the spring.

Chalcid larva undetermined. White, stout, hairless, with head and tail retracted but strongly flexed ventrally; dorsal prominences rudimentary, as a pair of lips, not or scarcely protrusible, at the junction of the segments. Head transversely cordiform, with the frontal lobe prominent on each side; jaws not coloured. The only larva found was in a *Perichistus* cell the original occupant of which it had apparently destroyed. Unfortunately it failed to mature.

The Smooth Pea-gall.

There is considerable confusion in regard to these galls. Cameron and other authors seem to assume that they are formed by one species of *Rhodites*, *R. eglanteriae* Htg., but it has been found that two distinct species of *Rhodites* are to be reared from them (Niblett, 1943), and that the one most commonly obtained is not *eglanteriae* but appears to be indistinguishable from the fly reared from the Spiked Pea-gall, identified by Cameron with *Cynips nervosa* Curt. My own experience is unfortunately very limited, though I have 10 examples of *R. eglanteriae*, recognisable by its red legs and elongate radial cell, to 14 of *R. nervosus*, with dark legs and short radial cell with heavily clouded nervures. All are female. I have not been able, however, to separate the galls into two series, and in two instances both species emerged from the same gathering of galls, i.e. galls from the same place and on the same day, but not necessarily from the same bush. The inquiline and parasites noted cannot therefore be assigned definitely to either of these species but to the combination of them.

INQUILINE: *Perichistus caninae* Htg. The early stages of this species and the development of the cells within the gall have been briefly described above under *R. rosae*.

PARASITES: *Orthopelma brevicornis* Morl. I have only two examples of this species, both associated with *R. nervosus*, and the only Ichneumonid reared from these galls, though Cameron records *Hemiteles imbecilis* Gr. This experience would agree with that of Callan (1943).

Torymus auratus Fourc. Reared from small galls with thin walls, hence no doubt a parasite of the *Rhodites*.

Torymus sp. (? *viridis* Foerst.). With darker legs than the above, but the galls from which they had emerged were not noted. Cameron (1893) records also *T. congener* Foerst. and *T. eglanteriae* Mayr, neither of which appears in Morley's list (1910), or in his own 1901 paper, in which *Torymus viridis* Frst. and *Syntomaspis pubescens* Frst. are noted from these galls.

Eurytoma rosae Nees. The predacious habit of the larva upon those of *Perichistus* has been described above. By far the most abundant Chalcid reared from these galls.

Tetrastichus sp. One moderate-sized gall produced 12 (6 of each sex) of this little Chalcid. The thin even walls of the gall indicate that it must have been parasitic upon the *Rhodites* itself, or perhaps hyperparasitic through the *Torymus*. Of interest as being the only multiple parasite found, and the only internal feeder amongst the Chalcidid parasites.

The Spiked Pea-gall.

As remarked above, there is some doubt as to whether this gall is the peculiar product of a distinct species of *Rhodites* or whether the same species of fly does not sometimes give rise to a smooth gall apparently indistinguishable from that of *R. eglanteriae*. Niblett, 1943, unable to reconcile this fly with the description of any of the known species, has described it as a new species, *R. dispar*; but to my mind this action does not help, as the name is almost bound to fall as a synonym of one or other of the described species, or to prove to be a composite species, when the different species can be more certainly determined. In the present uncertainty I prefer to follow Cameron in assigning the Spiked Pea-gall to *R. nervosus* Curt., with the assumption that the same species may sometimes produce smooth galls apparently indistinguishable from those produced by *R. eglanteriae*. My material of this gall has been yet more limited and I have been successful in breeding but a single *Rhodites* from them. This specimen, however, does differ from those reared from smooth galls, in possessing three strong parallel carinae on the scutellum, a feature of Curtis's description, though such carinae in my specimens from smooth galls are either absent or but feebly indicated. Moreover the mesonotum is markedly flat across the basal half, while anteriorly the median and lateral lobes are separately convex, with the parapsidal furrows lying in shallow depressions. The wings have the areolet undeveloped. Curtis mentions the absence of the areolet in comparing it with *R. rosae*. How far these characters are individual, or how far they would be confirmed by a longer series, remains to be seen. At any rate my specimens from the smooth galls agree in having the mesonotum gently and evenly convex in both directions, as well as in the undeveloped scutellar ridges, though they exhibit considerable variation in the development of the areolet of the wing. Should the differences here noted prove constant, then the name *nervosus* Curt. would seem to be applicable to the fly from the spiked gall and to have priority over *rosarum* Gir. (Enslin), while the very similar form from the smooth galls would be without a name unless that of Niblett's composite species *dispar* be restricted to it.

From these spiked galls I have bred only the inquiline *Periclistus caninae* and two species of parasites, *Eurytoma rosae* (presumably) and a small unidentified Chalcid.

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BOOK NOTICES.

Aerobiology. (Pub. Am. Ass. Adv. Sci. : 17.) Edited by F. R. MOULTON. 8vo. Washington, 1942.

This book is the result of a symposium held in Chicago in September 1942 in connection with the celebration of the fiftieth anniversary of the founding of the University of Chicago, and forms an important contribution to this specialised field of investigation. The volume consists of two distinct parts, extramural aerobiology and intramural aerobiology. The contribution of most interest to entomologists is entitled "Insect population and migration in the air" by P. A. Glick.

Garden Pest Control. By A. G. L. HELLYER. pp. 120, 31 plates. Sm. 8vo. London (W. H. and L. Collingridge) (1944). Price 7s. 6d.

Primarily intended as a handy guide for amateur gardeners and allotment-holders, this book is written in simple non-technical language, and is divided under the five following headings which make for quick and easy reference : (1) Basic information regarding types of foes and methods of control; (2) the foes—pests and diseases; (3) the victims—fruits, vegetables and flowers; (4) the weapons—insecticides, fungicides, etc.; (5) a monthly calendar of routine measures.

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—, 1936, New species of Coccidae. *Trans. R. ent. Soc. Lond.* **84** : 901-936.

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